ON THE SKULL OF *OLIGOKYPHUS*

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Pp. 67–82 ; 1 *Plate* ; 17 *Text-figures*

BULLETIN OF

THE BRITISH MUSEUM (NATURAL HISTORY)

GEOLOGY Vol. 9 No. 4

LONDON : 1964

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 9, No. 4 of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued February, 1964 *Price Nine Shillings*

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By ALFRED WALTER CROMPTON

CONTENTS

SYNOPSIS

Kühne (1956) gave a reconstruction of the brain-case of *Oligokyphus*. A new reconstruction has been based upon small fragments of the skull ; it shows that the two right-angled bends in the ventral surface of the brain-case, described by Kühne, are present only in the particular specimen upon which his reconstruction was based and are due to post-mortem distortion.

There follows a discussion of the spatial relationship of the quadrate to the otic bones and to the squamosal in various cynodonts, both primitive and advanced. This indicates that in *Oligokyphus* the quadrate was *not* suspended from the hinder of the two compartments in the ventral surface of the squamosal, as suggested by Kühne, but from the lateral surface of the anterior process of the paroccipital process.

I. INTRODUCTION

Kühne (1956) described in great detail fragments of several skulls and post-cranial skeletons of the therapsid *Oligokyphus* Hennig 1922, all from the Liassic fissure " Mendip 14 " near Shepton Mallet in Somerset. His excellent monograph includes fairly complete reconstructions of this material. Thus *Oligokyphus* is better known than are many other therapsids of which material is abundant and well preserved.

Oligokyphus is one of the last survivors of the therapsids. Although it has a specialized dentition and many other features which preclude it from being ancestral to any known mammal, it is of the greatest importance for the understanding of the evolutionary trends in the mammal-like reptiles and for the interpretation of the transition from reptiles to mammals.

II. KÜHNE'S RECONSTRUCTION OF THE BRAIN-CASE

As reconstructed by Kühne (1956 : 57, text-figs. 17–20), the brain-case of *Oligokyphus* possesses several features which distinguish it from the brain-cases of all other known therapsids—especially the advanced forms *Bienotherium* Young 1940 (see Young 1947) and *Diarthrognathus* Crompton 1958—and of early mammals such as *Triconodon* Owen 1859 (see Kermack 1963). These are as follows :

(1) The ventral surface of the basioccipital is bent into a right angle, so that the morphologically ventral surfaces of the basisphenoid and of the anterior

part of the basioccipital lie in a vertical plane and face posteriorly. The basipterygoid processes are therefore directed vertically downwards rather than forwards.

(2) The junction of the vertically orientated ventral surface of the basisphenoid and of the horizontally orientated ventral surface of the parasphenoid also forms a right angle.

(3) The pituitary fossa opens forwards and slightly downwards.

(4) The supraoccipital forms a horizontal roof to the posterior part of the cranial cavity.

Kühne's reconstruction, however, introduces a major difficulty which was not discussed in his monograph. If, as he supposed, the basipterygoid processes of *Oligokyphus* were indeed directed ventrally, it would follow that the morphologically ventral surfaces of the posterior ends of the epipterygoids and pterygoids would also lie in a vertical plane. How, then, could they have joined on to the more anterior bones of the palate? (Kühne, unfortunately, did not attempt a reconstruction of the brain-case in lateral view.)

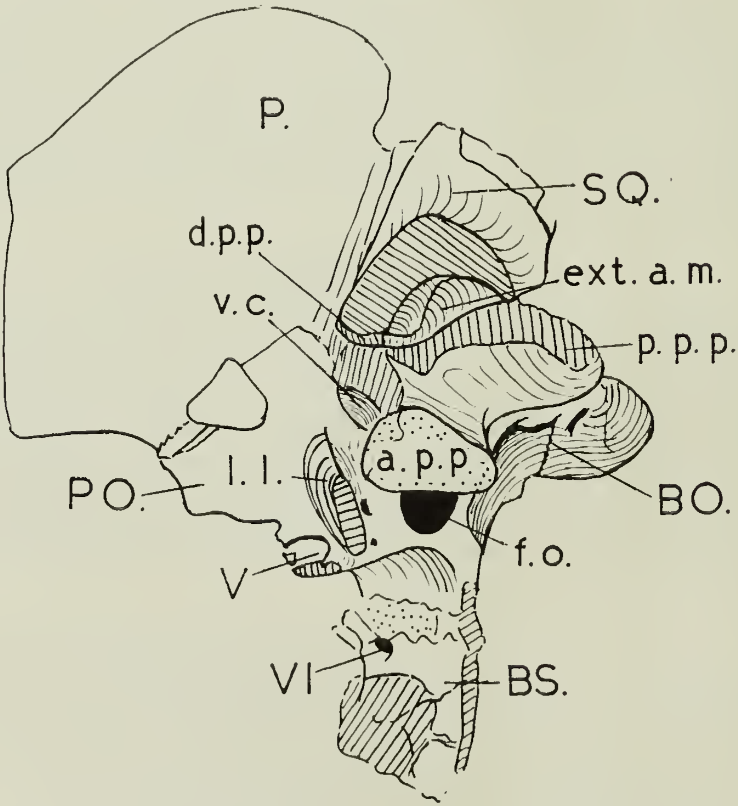
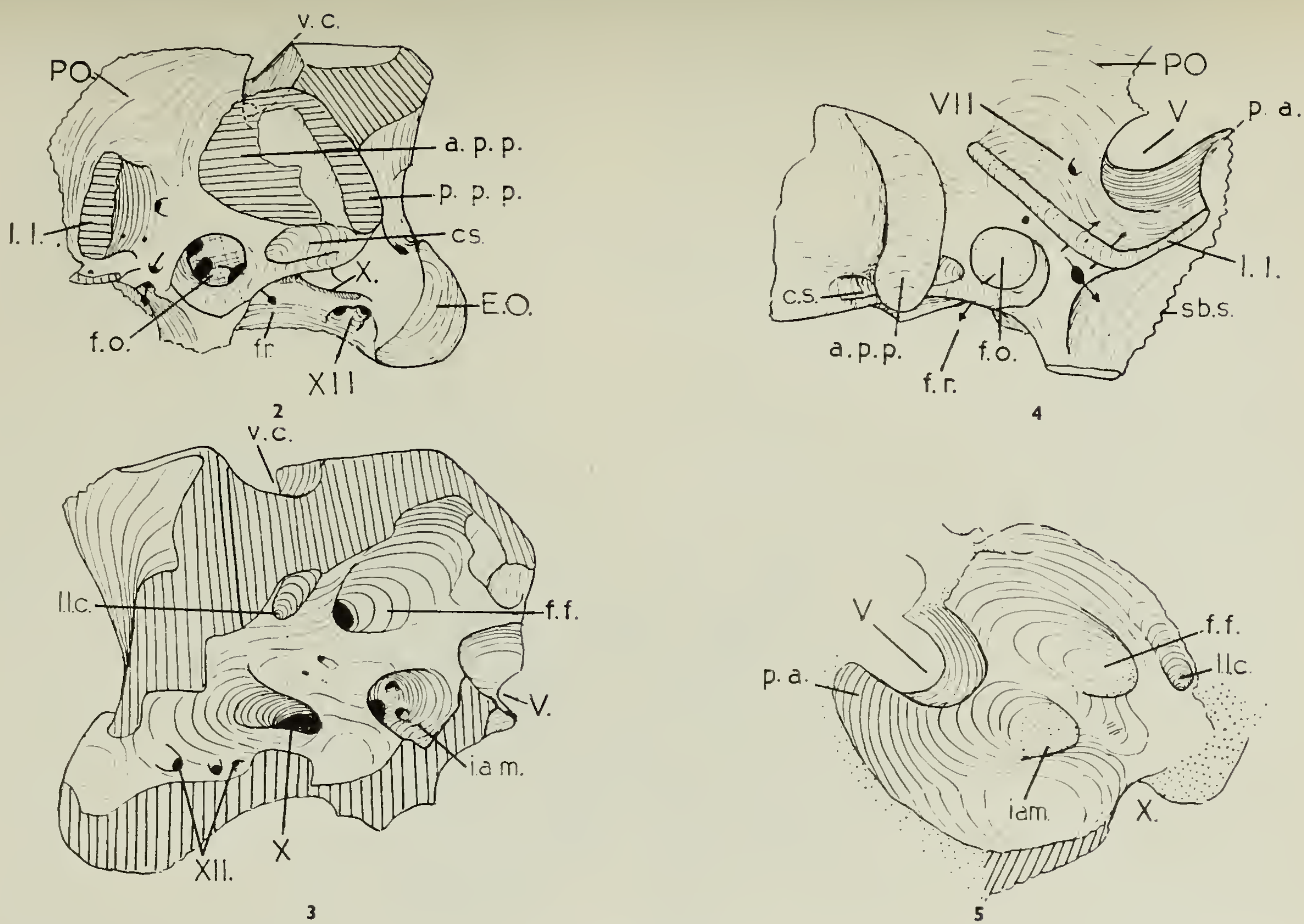


FIG. 1. *Oligokyphus* sp. Partly dislocated brain-case R.7090. Key to lettering, p. 82.



FIGS. 2–5. *Oligokyphus* sp. Fragments of brain-cases upon which the reconstruction of the brain-case, shown in Text-figs. 6–8, was partly based :
Fig. 2. External view of R.7110. Fig. 3. Internal view of the same. Fig. 4. External view of R.7109.
Fig. 5. Internal view of the same. Key to lettering, p. 82.

At this point it must be noted that Kühne's reconstruction of the hinder part of the skull was based largely upon one incomplete specimen (Brit. Mus. (Nat. Hist.) Palaeont. Dept. No. R.7090 ; Text-fig. 1), of which the bones seemed to be preserved in their natural articulation, not even partly separated. Such articulated skulls are rare among the *Oligokyphus* material.

I cannot agree that the arrangement of the individual bones in R.7090 is as it was in life. The specimen has several large cracks passing through it ; for example, there is a large transverse fracture through the basioccipital (BO.). Moreover, in many cases it is clear that adjacent bones have been separated from one another before fossilization, the best example of this being the wide separation of the squamosal (SQ.) from its contact with the anterior process of the paroccipital process (a.p.p.). Kühne observed that the lower surface of the squamosal bore a marked depression (d.p.p.), into which fitted—so he concluded—the dorsal surface of the anterior portion of the paroccipital process ; but pl. 9, fig. 4 of his monograph shows a distinct gap between those two elements, apparently filled with plaster. The presence of this gap suggests that in R.7090 the parietal (P.) and squamosal have been moved dorsally relative to the remainder of the specimen ; such movement could account for the vertical orientation of the morphologically ventral surface of the basisphenoid (BS.). The horizontal orientation of the supraoccipital appears also to be the result of dislocation. But, since the exact nature of the relative movement between its dorsal and ventral components cannot be ascertained, R.7090 should not be used as a basis upon which to reconstruct the brain-case of *Oligokyphus*.

III. NEW RECONSTRUCTION OF THE BRAIN-CASE (FROM FRAGMENTS)

The collection of *Oligokyphus* material in the British Museum (Natural History) includes several small fragments of the brain-case and adjacent elements, beautifully preserved and apparently not much distorted. Kühne listed these (p. 46) and figured some of them. Two of them are shown in Text-figs. 2–5.

Using these fragments, I have prepared a new reconstruction of the brain-case (together with certain associated bones such as the quadrate and squamosal) ; this reconstruction is shown in Text-figs. 6–8. The task was difficult because the fragments represent several individuals of unequal size. Pieces from different parts of the region were therefore photographed from the same angle ; drawings were prepared from the photographs, the enlargement of the drawings being adjusted to compensate for the varying sizes of the individuals concerned. The three views of the reconstructed brain-case were made by superimposing these drawings.

The lateral view (Text-fig. 6) is based mainly upon the fragments numbered R.7109 and R.7110 (Text-figs. 4 and 2 respectively). The ventral surface of the basioccipital is reconstructed from R.7113, the parietal from R.7090 and the squamosal from R.7088 and R.7090. The combined reconstruction based upon these fragments does *not* show two right-angled bends in the base of the skull ; a sagittal section of the ventral surface of the basioccipital and the basisphenoid would form an S-shaped curve, the ventral surface of the basisphenoid being lower than that of the basioccipital. Both R.7110 and R.7113 show a duct (v.c.) through the lateral wall of the brain-case just above the paroccipital process (Text-figs. 2, 6), its external opening lying close to the anterior opening of the post-temporal fenestra (pt.f.). According to Brink (1955), a similar foramen is present in cynodonts (Text-figs. 10, 12) ; while Ginsburg (1962 : 188–189) described a similar duct in the tritylodontid *Likhoelia ellenbergeri*, and named it the floccular canal.

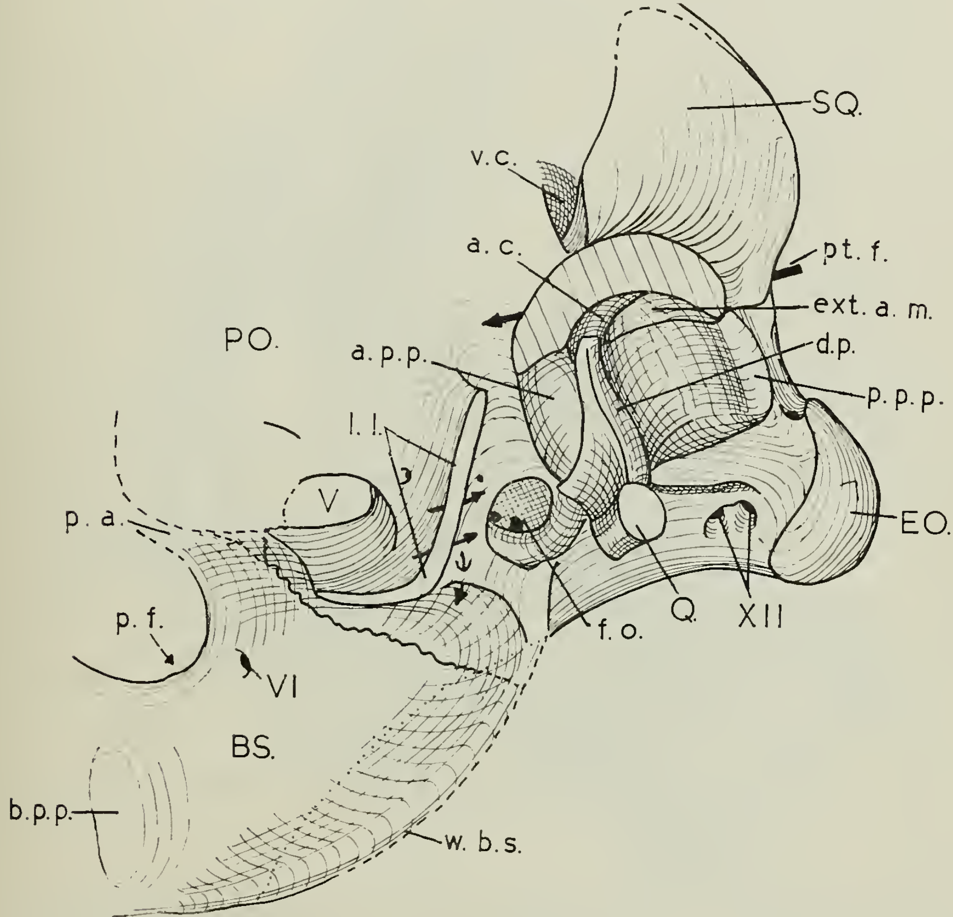


FIG. 6. *Oligokyphus* sp. Reconstruction of the brain-case, in lateral view. Key to lettering, p. 82.

The internal view of the reconstructed brain-case (Text-fig. 7) is based mainly upon R.7090, R.7109 (Text-fig. 5), R.7110 (Text-fig. 3), R.7113 and R.7242. It affords no evidence to support either of Kühne's beliefs, that there were two right-angled bends in the base of the skull and that the supra-occipital (SO.) formed a horizontal roof to the posterior part of the cranial cavity. The duct through the cranial wall above the paroccipital process opens internally just above and behind the floccular fossa (f.f.) ; in R.7090, where the external opening of this duct is

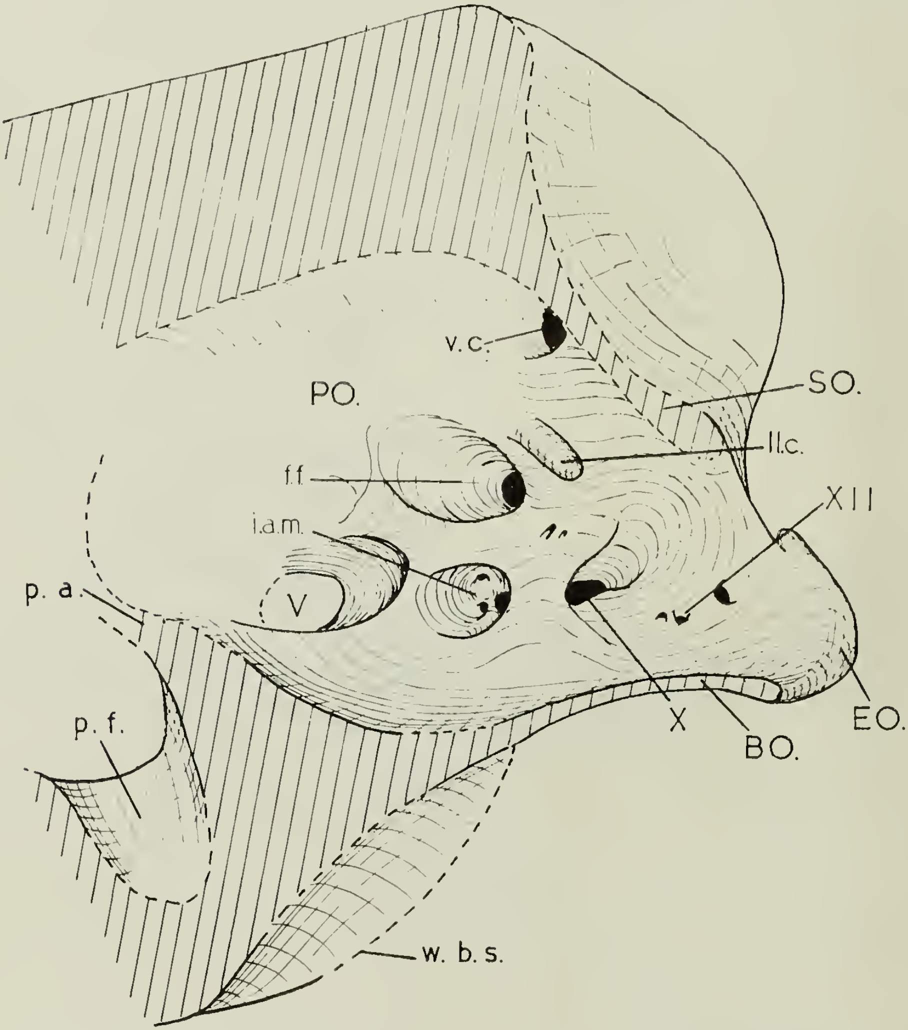


FIG. 7. *Oligokyphus* sp. Reconstruction of the brain-case : section in the sagittal plane, to show the interior.
Key to lettering, p. 82.

clearly visible (Text-fig. 1), its internal opening has been obscured by the downward displacement of the supraoccipital.

The ventral view (Text-fig. 8) is based mainly upon R.7088, R.7109, R.7113 and R.7242. The most marked feature of the *Oligokyphus* basisphenoid is that its ventro-lateral edges are drawn downwards and outwards as two thin sheets or wings of bone (w.b.s.), which form a partial floor to the cavum epiptericum on either side of the skull. This condition contrasts with that found in cynodonts, where the ventrolateral edges of the basisphenoid project for only a short distance.

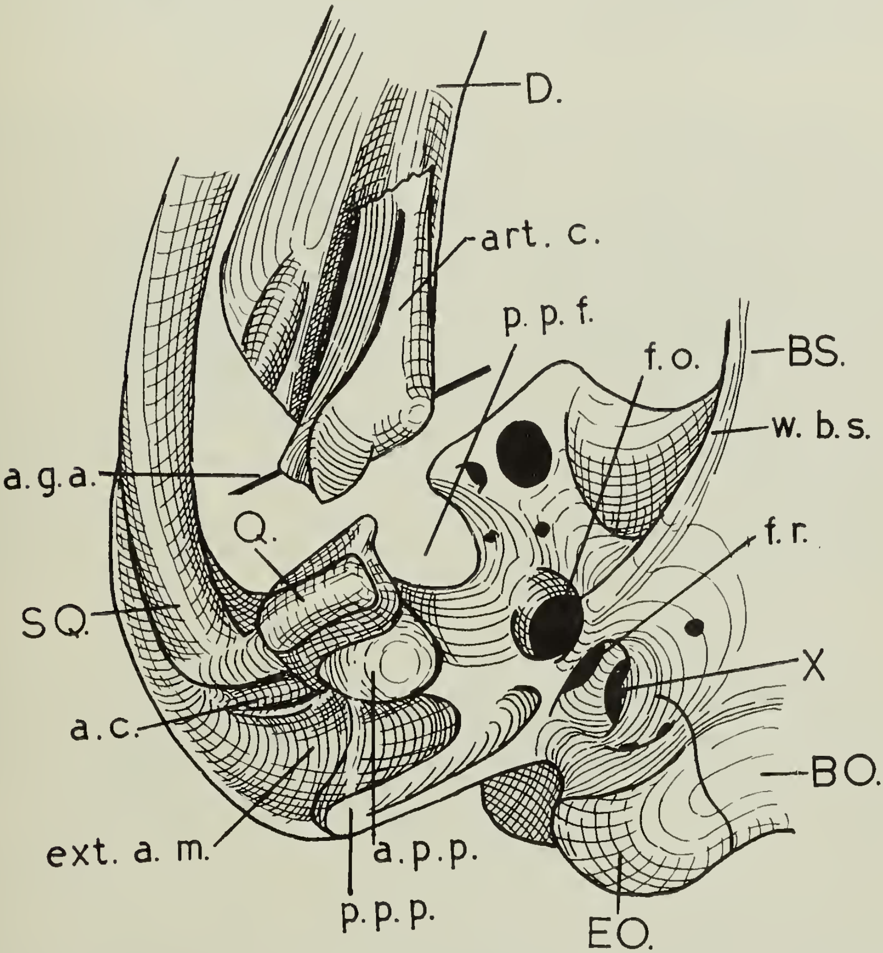


FIG. 8. *Oligokyphus* sp. Reconstruction of the brain-case and hind part of the lower jaw, in ventral view.
Key to lettering, p. 82.

In general, however, the brain-case of *Oligokyphus* (as reconstructed in Text-figs. 6–8) does not differ greatly from the brain-cases of primitive cynodonts, advanced cynodonts, *Bienotherium* or *Diarthrognathus*. Comparison is facilitated by Text-figs. 9–17, which show the brain-cases of a procynosuchid, *Cynognathus* and *Oligokyphus* in ventral, lateral and occipital views.

Ginsburg (1962) published an account of a new tritylodontid, *Likhoelia ellenbergeri* Ginsburg 1961, from the upper part of the Red Beds (Upper Trias) of Basutoland. The material included an almost complete brain-case, in which the ventral surface of the basioccipital was not bent into a right angle. Ginsburg remarked upon the ventral keel of the basisphenoid of *Oligokyphus* and concluded that it was sufficient to rotate the whole posterior part of the skull of *Oligokyphus* through some 30° to obtain a cranium very like those of *Bienotherium* and of *Likhoelia*.

IV. THE ANTERIOR WALL OF THE PROOTIC

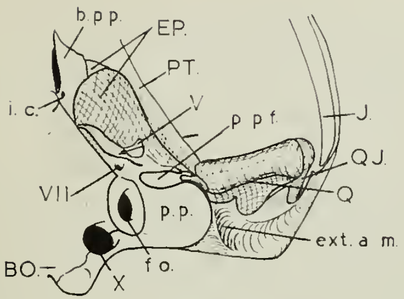
In Text-figs. 6 and 7 the anterior wall of the prootic (PO.) of *Oligokyphus* has been reconstructed in such a way that it completely encloses a foramen (V.) for the trigeminal nerve. There is no conclusive evidence for this reconstruction, for in none of the skull fragments is the anterior border of the prootic preserved entire.

The anterior border of the prootic is best preserved in R.7109 (Text-fig. 4), where the antero-ventral corner of the bone, above the opening for the trigeminal nerve, is directed downwards and forwards towards the ossified pila antotica (p.a.). The dorsal surface of the pila antotica is smooth except for its postero-dorsal tip, which has a broken surface ; this may indicate that the antero-ventral corner of the prootic, above the trigeminal nerve, extended downwards and forwards in life towards the pila antotica and thus enclosed the nerve. In the early mammal *Morganucodon* the anterior border of the prootic formed a foramen for the trigeminal nerve (Kermack & Mussett 1958). In *Likhoelia* the anterior lamina of the prootic appears to enclose a foramen pseudovale, although it may be that the anterior border of the foramen in question is formed by the epipterygoid ; the sutures cannot be distinguished in this region.

V. THE POSITION OF THE QUADRATE

The condyle of the quadrate (Q.) (Text-figs. 6, 8, 17) supports a vertical sheet of bone which runs more or less transversely. The upper margin of this sheet expands in the horizontal plane to form a smooth concave surface, facing upwards ; at its lateral end, however, it rises into the high " peg-like process " (d.p.) mentioned by Kühne (pp. 39, 40). The smooth concave surface, lying immediately above the quadrate condyle, is confluent with the medial surface of the peg-like process.

Kühne claimed (p. 45) that there was no place on the periotic that could have served for the attachment of the quadrate. But the ventral surface of the posterior part of the squamosal bears an ectotympanic cavity which is divided into two compartments (Text-fig. 8, ext.a.m., a.c.). He therefore concluded that " . . . there is no other possible place for the quadrate and the quadrato-jugal than the anterior end of the two compartments . . ." ; that is, the anterior compartment would be for the quadrato-jugal and the posterior compartment for the quadrate.



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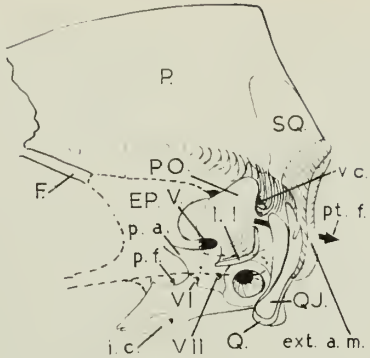

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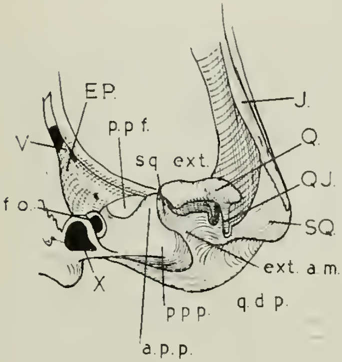

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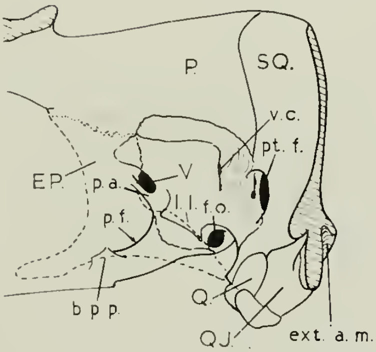

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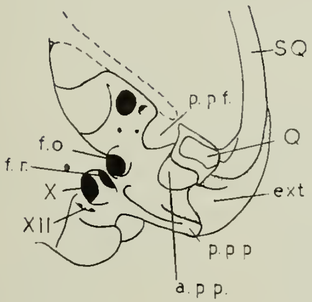

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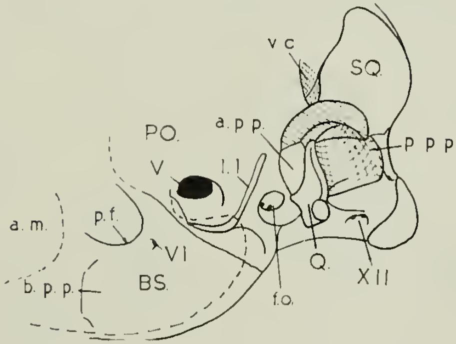


14

Figs. 9–14. Comparisons of the brain-cases of cynodonts and of *Oligokyphus* in ventral and lateral views :

Figs. 9, 10. *Leavachia* (a procynosuchid). Figs. 11, 12. *Cynognathus.*

Figs. 13, 14. *Oligokyphus.*

Key to lettering, p. 82.

Kühne also pointed out (p. 40) that the dorsal surface of the quadrate and the dorsal surface of the peg-like process had no corresponding articular surfaces on the squamosal. Because, in particular, the posterior compartment of the ectotympanic cavity did not possess an articular surface for the dorsal surface of the quadrate, he decided that the connection between the quadrate and the squamosal must have been maintained by ligaments.

But the ectotympanic cavity on the ventral surface of the squamosal is continuous with the external auditory meatus. If the quadrate really had been attached to the squamosal by ligaments, with its peg-like process fitting into the posterior compartment of the ectotympanic cavity, then it would partly have blocked the external auditory meatus. Further, with the quadrate in the position suggested by Kühne, the glenoid facet of the articular complex would not have reached the quadrate condyle ; it would have been prevented from doing so by the anterior process of the paroccipital process, which lies antero-medial to the posterior compartment (Text-fig. 8).

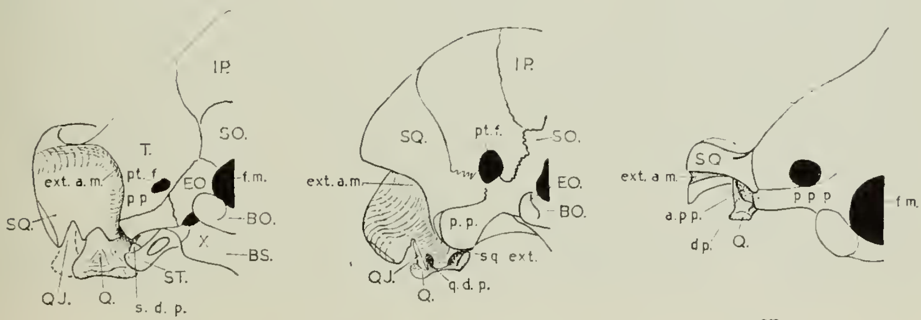
A study of the relative positions of the articular and the quadrate in cynodonts throws some light on the probable position of the quadrate in *Oligokyphus*.

In the procynosuchids of the Upper Permian (Text-figs. 9, 10, 15) the quadrate is suspended partly from the squamosal and partly from the paroccipital process ; the latter (Text-fig. 9, p.p.) is fairly slender antero-posteriorly. The quadrate and quadrato-jugal fit into a shallow pocket in the anterior surface of the squamosal, and the ventral edge of the squamosal is notched. The medial surface of the quadrate abuts against the antero-lateral surface of the paroccipital process ; this feature, which has been observed in several procynosuchids and other early therapsids, is seen well from behind (Text-fig. 15). The antero-medial surface of the quadrate meets the quadrate rami of the pterygoid (PT.) and epipterygoid (EP.). The external auditory meatus (ext.a.m.) of early cynodonts is not deep, but its course is clearly shown in Text-figs. 9 and 15 ; it follows the dorsal surface of the squamosal, passes above the medial quadrate condyle, runs vertically downwards, and ends just by the lower surface of the postero-lateral corner of the paroccipital process. Cox (1959) named this corner the tympanic process in anomodonts. The stapes of a procynosuchid is exemplified by the specimen of *Leavachia microps* (Broom & Robinson 1948) illustrated in Text-fig. 15, in which the bone (ST.) is preserved in position. It bears a distinct blunt process, directed laterally, which probably supported a cartilaginous extra-stapedial process (Parrington 1946) ; it has also a well preserved dorsal process (s.d.p.).

In later cynodonts, e.g. *Cynognathus* of the Lower Trias (Text-figs. 11, 12, 16 ; Pl. 1), several significant developments have taken place. It can be seen from behind (Text-fig. 16) that the depth of the squamosal has increased greatly and that the external auditory meatus has also become deeper. Ventral and occipital views show that a thin flange of the squamosal (sq.ext.) extends downwards and forwards, completely covering the lateral surface of the paroccipital process ; the latter is therefore no longer in contact with the greatly reduced quadrate. The external auditory meatus has been extended downwards and forwards by the extension of the squamosal in that same direction, and it ends just above the medial condyle of the quadrate ; its most ventral part lies lateral to the centre of the ventral part of the lateral surface of the paroccipital process (Text-fig. 11). The posterior surface of the quadrate, above the medial condyle, is slightly concave. A short flange orientated in an antero-posterior plane (Text-fig. 16, q.d.p.) extends upwards from the lateral side of the quadrate, its postero-dorsal corner fitting into a pocket in the ventral surface of the squamosal. The quadrato-jugal (QJ.) consists mainly of a high, flat sheet, also orientated antero-posteriorly, lying against the quadrate (Text-fig. 12) ; ventrally it is fused with the quadrate above the lateral condyle. On its medial side the posterior edge of the vertically orientated quadrato-jugal lies against a ventrally directed process of the squamosal (Text-figs. 11, 16) ; a shallow notch in the ventral surface of the squamosal contains only the postero-dorsal tip of the quadrato-jugal. A stereo-photograph of this region of the skull of *Cynognathus* (Pl. 1) may help to explain the relationship of the quadrate to the squamosal.

In *Cynognathus* (Text-fig. 11) the lateral region of the paroccipital process is wider antero-posteriorly than in procynosuchids. The ventral surface of the paroccipital process of *Cynognathus* can be divided into two regions, a bulbous anterior region (a.p.p.) and a flat posterior region (p.p.p.) ; the quadrate lies lateral to the former. In *Oligokyphus* (Text-fig. 13) the paroccipital process ends laterally in two distinct processes, a bulbous anterior process and a narrow posterior process, separated by a shallow depression. It is reasonable to conclude that the bulbous anterior process of the paroccipital process of *Oligokyphus* is homologous with the bulbous anterior region of the paroccipital process of *Cynognathus*.

One of the major differences between *Oligokyphus* and cynodonts such as *Cynognathus* is in the height of the squamosal, which is much reduced in *Oligokyphus* ; this is best shown by a comparison of the respective occipital views (Text-figs. 16, 17). There is a similar reduction in *Diarthrognathus*. The squamosal of *Oligokyphus*, because of this reduction in height, does not cover the lateral surface of the paroccipital process (Text-fig. 6).



FIGS. 15–17. Comparison of the brain-cases of cynodonts and of *Oligokyphus* in occipital view :
Fig. 15. *Leavachia*. Fig. 16. *Cynognathus*. Fig. 17. *Oligokyphus*.
Key to lettering, p. 82.

As the quadrate of advanced cynodonts is suspended from the squamosal, a reduction of the ventral part of the latter would cause the quadrate to lose its only firm attachment. If, however, the quadrate migrated very slightly towards the mid-line, it could establish alternative contact with the lateral surface for the anterior part of the paroccipital process.

In *Oligokyphus* the quadrate has a smooth concave dorsal surface and a dorsally directed peg-like process on its lateral surface. This peg-like process is perhaps homologous with the dorsally directed process above the lateral condyle of the cynodont quadrate. The concave dorsal surface of the *Oligokyphus* quadrate could have evolved by the further development of the concavity which, in *Cynognathus*, is already present in the posterior surface of the quadrate above the condyle.

The smooth concavity of the *Oligokyphus* quadrate, formed by its dorsal surface and by the medial surface of the peg-like process, fits perfectly against the lateral and ventro-lateral surface of the bulbous anterior head of the paroccipital process (Text-figs. 6, 8, 17). Further, this would be the expected position of the quadrate if, in the ancestors of *Oligokyphus*, the squamosal had been reduced in height and no longer suspended the quadrate. The shape of the quadrate in *Oligokyphus* confirms that it was supported by the anterior process of the paroccipital process. If the quadrate be placed in this position the transverse axis of its condyle is oblique to the sagittal plane (Text-fig. 8), not perpendicular thereto as is usual in cynodonts (Text-figs. 11, 13) ; this accords with the oblique orientation of the articulating surface of the articular. In Text-fig. 8 the articular complex and the back end of the dentary are shown from below ; the transverse axis through the glenoid (a.g.a.) is parallel to that through the quadrate condyle.

In *Cynognathus* the external auditory meatus lies entirely within the squamosal, with its lower part lateral to the centre of the lateral surface of the paroccipital process. In *Oligokyphus*, however, the squamosal is reduced and can no longer delimit the external auditory meatus lateral to the paroccipital process ; but there is a hollowing in the lateral surface of the paroccipital process, continuous with the external auditory meatus in the squamosal, which presumably helped to delimit the lower part of the meatus. It is this hollowing which divides the paroccipital process into anterior and posterior processes. The external auditory meatus of *Oligokyphus* would therefore have ended behind the medial condyle of the quadrate, just as in cynodonts. These arguments seem to support the view that the quadrate was not suspended from the posterior compartment on the ventral surface of the squamosal. It is possible, however, that the dorsal end of the peg-like process on the quadrate may have extended into the anterior compartment.

The advanced therapsid (early mammal ?) *Diarthrognathus* seems also to have a lower squamosal. The withdrawal of the quadrate into the middle ear in early mammals may be correlated with a reduction of the paroccipital process.

VI. ACKNOWLEDGMENTS

I should like to thank Dr. E. I. White, F.R.S., Keeper of Palaeontology, for allowing me to study the *Oligokyphus* material in the British Museum (Natural

History). I am grateful also for the help which I received from Dr. White and from the staff of his Department.

I wish to acknowledge bursaries from the Royal Society and the Nuffield Foundation and from the South African C.S.I.R., without which this work could not have been undertaken.

My thanks are also due to Dr. F. R. Parrington, F.R.S., for reading the manuscript and for his encouragement and advice.

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KEY TO LETTERING

a.c.	anterior compartment
a.g.a.	axis of the articular glenoid
a.p.p.	anterior process of the paroccipital process
art.c.	articular complex
BO.	basioccipital
b.p.p.	basipterygoid process
BS.	basisphenoid
c.s.	cavity for stapedial muscle
D.	dentary
d.p.	dorsal process of the quadrate
d.p.p.	depression in the squamosal for the paroccipital process
EO.	exoccipital
EP.	epipterygoid
ext.a.m.	external auditory meatus
F.	frontal
f.f.	floccular fossa
f.m.	foramen magnum
f.o.	fenestra ovalis
f.r.	fenestra rotunda
i.a.m.	internal auditory meatus
i.c.	internal carotid foramen
IP.	interparietal
J.	jugal
l.l.	lateral lamina
l.l.c.	depression for the lateral lobe of the cerebellum
P.	parietal
p.a.	pila antotica
p.f.	pituitary fossa
PO.	prootic
p.p.	paroccipital process
p.p.f.	pterygo-paroccipital foramen
p.p.p.	posterior process of the paroccipital process
PT.	pterygoid
pt.f.	post-temporal fenestra
Q.	quadrate
q.d.p.	dorsal process of the quadrate
QJ.	quadrato-jugal
s.b.s.	suture with the basisphenoid
s.d.p.	dorsal process of the stapes
SO.	supraoccipital
SQ.	squamosal
sq.ext.	ventral extension of the squamosal
ST.	stapes
T.	tabular
v.c.	venous canal
w.b.s.	wing of the basisphenoid
V	foramen for the trigeminal nerve (incisura prootica)
VI	foramen for the sixth cranial nerve
VII	foramen for the seventh cranial nerve
X	jugular foramen
XII	foramina for the twelfth cranial nerve

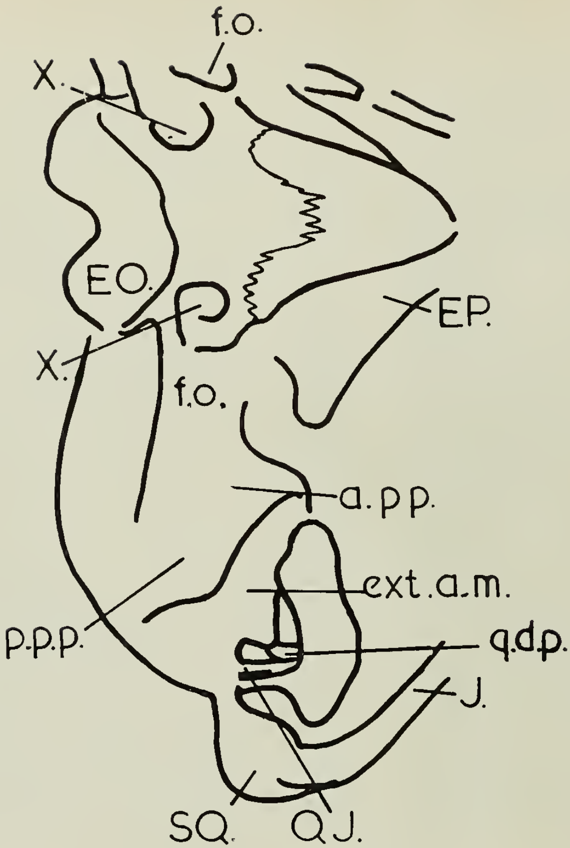

PLATE I

Cynognathus sp.
Stereo-photographs of the hind part of the skull, in ventral view. × 1.25 approx.
Key to lettering, p. 82.